RESEARCH ARTICLE

Halyomorpha halys and its egg parasitoids *Trissolcus japonicus* and *T. mitsukurii*: the geographic dimension of the interaction

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Abstract

Halyomorpha halys (Stål) (Hemiptera, Pentatomidae) was accidentally introduced to North America and Europe, becoming a key pest of many important crops. In its native range, it is attacked by egg parasitoids, including *Trissolcus japonicus* (Ashmead), considered to be the main species, and *T. mitsukurii* (Ashmead) (Hymenoptera, Scelionidae). *Trissolcus japonicus* was detected in North America in 2014 and Europe in 2017, while *T. mitsukurii* was detected in Australia in the early 20th century and in Europe in 2016. Both species now appear established in the new areas. The present study used the MaxEnt algorithm to clarify the geographic dimension of the potential interaction between *H. halys* and these two parasitoid species, and to indicate where the release of one or the other parasitoid species is more likely to be effective. We found that the suitability for the two parasitoids overlaps the *H. halys* native range completely. In invaded areas, *T. japonicus* showed higher potential habitat suitability at the global scale, compared to *T. mitsukurii*, and also higher potential suitability at lower latitudes at continental and national scales. These results can substantially improve the effectiveness of biological control against *H. halys*, by targeting the releases of parasitoids to the areas where each species is most likely to succeed.

Introduction

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera, Pentatomidae), is a polyphagous and invasive pest native to Asia (China, Japan, Korea, and Taiwan) (Lee et al. 2013), which was accidentally introduced to North America and Europe in the late 1900s and early 2000s, respectively (Leskey and Nielsen 2018). In invaded areas, it has become a key pest causing severe economic losses on many important crops (e.g., Gariepy et al. 2014; Maistrello et al. 2017; Bosco et al. 2018; Leskey and Nielsen 2018; Moore et al. 2019). It was also detected in Chile (Faúndez and Rider 2017) and often intercepted at the Australian and New Zealand borders (Charles et al. 2019; Horwood et al. 2019). In addition, possible further spread in North America, Europe, and in many regions in the Southern Hemisphere has been suggested (Kriticos et al. 2017), and simulations with climate change scenarios indicate that *H. halys* has the potential to further expand its range (Stoeckli et al. 2020).

Crop protection in the invaded areas mainly relies on chemical control based on broad-spectrum insecticides, which are not always able to keep *H. halys* infestations below the economic injury level. This failure is mainly due to multiple factors, such as the low direct and residual toxicity to *H. halys* of several insecticides. Moreover, the frequent application of insecticides, even considering the restrictions in place for the use of some broad-spectrum active ingredients, may cause secondary pest outbreaks, in addition to negative effects on human and environmental health (Leskey and Nielsen 2018). Therefore, biological control has been considered a promising alternative to chemical control in IPM programs, with an emphasis on egg parasitoids that are the main natural enemies in the native range (Lee et al. 2013).

Both in North America and in Europe, few native parasitoids were found to develop on *H. halys* eggs successfully (Abram et al. 2017; Balusu et al. 2019b, a; Costi et al. 2019; Konopka et al. 2019; Stahl et al. 2019c; Moraglio et al. 2020; Scaccini et al. 2020). In Europe, the generalist *Anastatus bifasciatus* (Geoffroy) (Hymenoptera, Eupelmidae) was the main species emerging from both field-laid and sentinel *H. halys* egg masses in Italy and Switzerland (Haye et al. 2015a; Roversi et al. 2017; Costi et al. 2019; Moraglio et al. 2020), while *Trissolcus kozlovi* Rjachovskij (Hymenoptera, Scelionidae) was a promising but rare parasitoid emerging from *H. halys* eggs in northern Italy (Scaccini et al. 2020; Moraglio et al. 2021a; Zapponi et al. 2021). Both these native parasitoids were considered for an augmentative release strategy, but without effectively suppressing the pest so far (Stahl et al. 2019a; Moraglio et al. 2021b; Iacovone et al. 2022).

Adventive populations of *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae), a species that is considered the main parasitoid of *H. halys* eggs in China and

Japan (Yang et al. 2009; Lee et al. 2013; Zhang et al. 2017; Kamiyama et al. 2022), have been found both in North America and in Europe (Talamas et al. 2015; Abram et al. 2019; Stahl et al. 2019b). Additionally, adventive populations of *Trissolcus mitsukurii* (Ashmead), another egg parasitoid of *H. halys* in Japan (Arakawa and Namura 2002; Arakawa et al. 2004; Kamiyama et al. 2022), have been recently found in Europe (Sabbatini Peverieri et al. 2018; Scaccini et al. 2020; Bout et al. 2021). These two Asian species are candidates for classical biological control in the invaded range (Charles et al. 2019; Lara et al. 2019; Haye et al. 2020; Sabbatini Peverieri et al. 2020, 2021; Giovannini et al. 2022). In addition to being field released in some areas, *T. japonicus* is now established in North America, Switzerland, and Italy, where *T. mitsukurii* is also established, and both species are now spreading to other countries in Europe (Lowenstein et al. 2019; Milnes and Beers 2019; Scaccini et al. 2020; Zapponi et al. 2020, 2021; Bout et al. 2021; Dieckhoff et al. 2021; Rot et al. 2021; Mele et al. 2022).

Despite the great interest in this parasitoid-host interaction, many aspects are still poorly investigated. One of these aspects is the geographic dimension of this interaction, which is crucial for planning parasitoid releases because their success largely depends on the released species' local suitability. Some studies analyzed the potential distribution of *H. halys* at both global (Zhu et al. 2012, 2016; Haye et al. 2015b; Kriticos et al. 2017) and local scales (Zhu et al. 2017; Malek et al. 2018; Tytar and Kozynenko 2020; Streito et al. 2021), and a few others focused on the potential distribution of *T. japonicus* (Avila and Charles 2018) and of *T. mitsukurii* (Yonow et al. 2021). However, none explored the spatial dimension of the *H. halys*–parasitoid interactions.

The present study has the ambition to fill this gap, focusing specifically on the spatial overlap in suitability for *H. halys* and its parasitoids. Habitat suitability is necessary for establishing viable populations and thus for activating interspecific interactions, and so we adopted a data-driven approach based on distribution models and compared suitable areas at three geographical scales: global, continental, and national. This approach will be able to identify the areas where the risk of *H. halys* invasion is high, where such invasion can be effectively countered by the natural spread or augmentative release of its parasitoids, and where the release of *T. japonicus* is expected to be more effective than that of *T. mitsukurii*, and vice versa. These results can substantially improve the effectiveness of the biological control against this invasive pest, driving the release of parasitoids toward the areas where each species has the highest probability of success.

Materials and methods

Source of data

Geographic records of distribution of *H. halys* were retrieved from Global Biodiversity Information Facility (GBIF.org 2022). Geographic records of *T. japonicus* and *T. mitsukurii* were retrieved from GPS latitude and longitude coordinates of: i) monitoring sites of DISAFA (University of Turin, Italy) and DAFNAE (University of Padova,

Italy), ii) available data on Hymenoptera Online database (HOL 2021), and iii) literature data (Suppl. material 1: table S1). Localities lacking geographic coordinates were georeferenced using Google Maps. Records with doubtful species identification, unspecified or unknown localities were deleted. In localities where *T. japonicus* was used in augmentative release programs as a biological control agent (BCA) of *H. halys*, data for a year were considered valid if confirmed by observations during the following spring-summer, indicating wasp overwintering after the release. These various sources provided a total of 14,489, 393, and 356 point locations recorded for *H. halys*, *T. japonicus* and *T. mitsukurii*, respectively (Suppl. material 4: fig. S1).

Species distribution modelling

In order to verify the absence of potential divergences in the climatic niches of populations in primary and secondary ranges, which are sometimes introduced by bottleneck effects in introduced populations, we analyzed the climatic preference of the three species across their distribution ranges (Fig. 1). The results suggested that we should try to model the distribution of the three species using the entire global dataset rather than considering native and invaded ranges separately.

We used the distribution data for modeling habitat suitability for *H. halys*, *T. japonicus*, and *T. mitsukurii* at three spatial scales. All three species' global data were used to fit the models at the three scales. These models were fitted with three different spatial resolutions and projected into three different geographic areas. The maps were obtained from data combined and processed at different resolutions. Therefore, the global, European and Italian scale maps are the result of different processing. We used environmental predictors with a resolution of 10 minutes of geographic degrees (i.e., pixels about 20 km large) for predicting the habitat suitability at the global scale, 5 minutes (i.e., about 10 km) for the European scale, and 2.5 minutes (i.e., about 5 km) for the Italian scale. In order to mitigate the geographical bias associated with the non-random process of data collection, presence data were thinned to remove duplicate points in the pixels (Verbruggen et al. 2013). This multi-scale approach provided practical recommendations for managing the *H. halys* invasion and simultaneously overcoming the 'tyranny of the local' (Groves 2003), which consists of overlooking important areas at the large scale when reserves are planned locally.

We used several parameters representing climate, land morphology, land cover, and water availability as predictor variables. Climate variables were downloaded from the WorldClim 2.1 databank (Fick and Hijmans 2017). We selected a subset of non-correlated climatic variables for fitting the models by calculating the variance inflation factor (VIF) (Belsley 1991) and excluding those with VIF ≥ 5 (Dormann et al. 2013). Thus, we used eight, seven, and eight climatic variables at global, continental, and national scales, respectively. Land morphology variables were calculated from the altitude information associated to the WorldClim climatic data (Fick and Hijmans 2017). In particular, we calculated slope, roughness, eastness (calculated as the sine of terrain aspect), and northness (cosine of terrain aspect) (Kumar et al. 2006) for each pixel
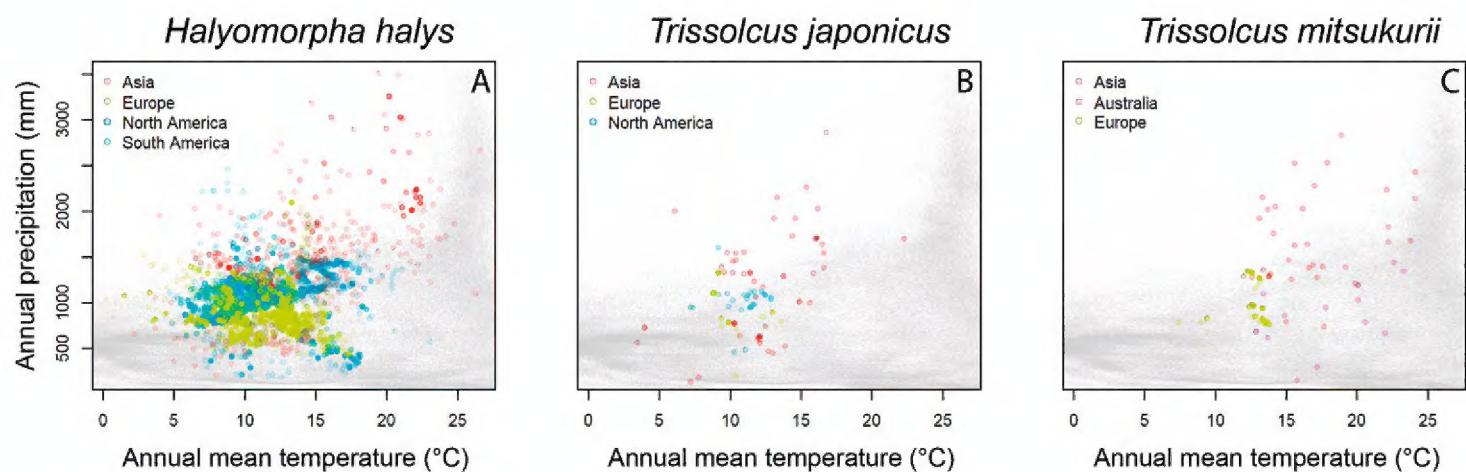
Figure 1. Climatic preferences of *Halyomorpha halys* (**A**), *Trissolcus japonicus* (**B**), and *T. mitsukurii* (**C**) in the native range (i.e., Asia) and invaded range. Colored dots represent the climatic conditions in the species presence sites and gray shade indicates the climatic conditions available across the species distribution.

by comparing elevation values of the pixel with those of the eight surrounding pixels. The land cover was downloaded from the GLC2000 database (European Commission Joint Research Centre 2003), which is available at the resolution of 1 km at Equator. Data on water availability were extracted from the Digital Global Map of Irrigation Areas (Siebert et al. 2013). In addition, for the two parasitoids, we incorporated the effect of the interaction with *H. halys* by adding the suitability for the stink bug as a predictor. Each variable was resampled at the three resolutions, tested for collinearity (see Suppl. material 2: table S2), and used for fitting and projecting the models.

The habitat suitability for the three species at the different scales was calculated using the MaxEnt algorithm (Phillips et al. 2004, 2006). MaxEnt minimizes the relative entropy between the probability densities in the covariate space estimated from the presence data and from the background (Elith et al. 2011). In order to correctly define unsuitable conditions, we defined the background conditions by selecting a number of random points across the study area (i.e., the globe) equal to five times the number of presence points. In order to account for the uncertainty in the definition of the background conditions associated with the randomicity of the background points, we repeated the analysis 100 times and generated a final consensus calculating the average value from the 100 models. All the models were 10-fold cross validated by deriving the Area Under the ROC Curve (AUC) value (Fielding and Bell 1997; Faraggi and Reiser 2002) and the Boyce index (Boyce et al. 2002). The AUC value can be interpreted as the probability that a presence site, randomly chosen from the dataset, has a higher predicted value than an absence site (Elith et al. 2006). The Boyce index measures how much model predictions differ from random distribution of the observed presences across the prediction gradients and is an appropriate metric for presence-only models (Hirzel et al. 2006).

To derive discrete categories from the continuous values of habitat suitability, we used a data-driven multi-thresholds approach (Nenzén and Araújo 2011). For each model we applied five different binarization criteria. First, the highest threshold at which there is no omission (Cantor et al. 1999). Second, the threshold at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is highest

(Cantor et al. 1999). Third, the threshold at which sensitivity and specificity are equal (Fielding and Bell 1997). Fourth, the threshold at which the modeled prevalence is closest to the observed prevalence (Dormann et al. 2008). Fifth, the threshold at which the sensitivity of the model is equal to 0.5 (Cantor et al. 1999). These thresholds were used for dividing the suitability values in six categories of increasing suitability, from no suitability (not suitable according to all five criteria) to high suitability (suitable according to all five criteria).

In order to explore the geographic dimension of the interaction between *H. halys* and its parasitoids, we generated the 'host-parasitoids co-suitability maps' by overlapping the habitat suitability models of the three species. In these maps, pixels are categorized based on their contemporary suitability for *H. halys* and for the parasitoids. We defined: (1) areas with scarce suitability for all the three species, (2) areas with scarce suitability for *H. halys* but good suitability for one or (3) two parasitoids, (4) areas with good suitability for *H. halys* but scarce suitability for the two parasitoids, and (5) areas with good suitability for *H. halys* and for one or (6) two parasitoids. In addition, for clarifying which parasitoid has the highest probability of success in the different areas, we produced conflict maps by overlapping the habitat suitability of the two *Trissolcus* species. In particular, we defined areas with scarce suitability for both the two species, areas with good suitability for one species and scarce for the other, and areas with good suitability for both the species. In the host-parasitoids and in the parasitoids co-suitability maps, we defined pixels with scarce suitability as those considered suitable according to less than three criteria and defined good suitability pixels as those considered suitable according to three criteria or more. In addition, we summarized the overlaps at the three scales by continent/country/region as the percentage of surface in the different conditions. All the analyses, as well as these maps, were done in R (R Core Team 2021), using the packages dismo (Hijmans et al. 2021), raster (Hijmans 2022), rgdal (Bivand et al. 2022), rJava (Urbanek 2021), and usdm (Naimi et al. 2014).

Results

We obtained very robust habitat suitability models for all three species at all three scales (mean ± st. dev. AUC: 0.987 ± 0.01; Boyce index: 0.994 ± 0.09). At the global scale, the highest suitability for *H. halys* was estimated to occur in East Asia (which is the species' primary range), southern Europe, and eastern North America (Fig. 2A). Further areas with low or medium-low suitability were identified around the abovementioned core areas (in southern Asia, Europe, and North America) as well as in South America (from southern Brazil to northern Argentina and along the Chilean coast), in Australia (in the South-East and South-West of the country), and in New Zealand (both North and South Islands). Suitable areas for *T. japonicus* were limited to East Asia, southern Europe, and eastern North America, by and large following the same pattern of the core areas for *H. halys* (Fig. 2B). In contrast, suitable core areas for *T. mitsukurii* were limited to East Asia and southern Europe. However, additional areas with partial suitability occur in eastern North America, South America, Australia, and New Zealand (Fig. 2C).
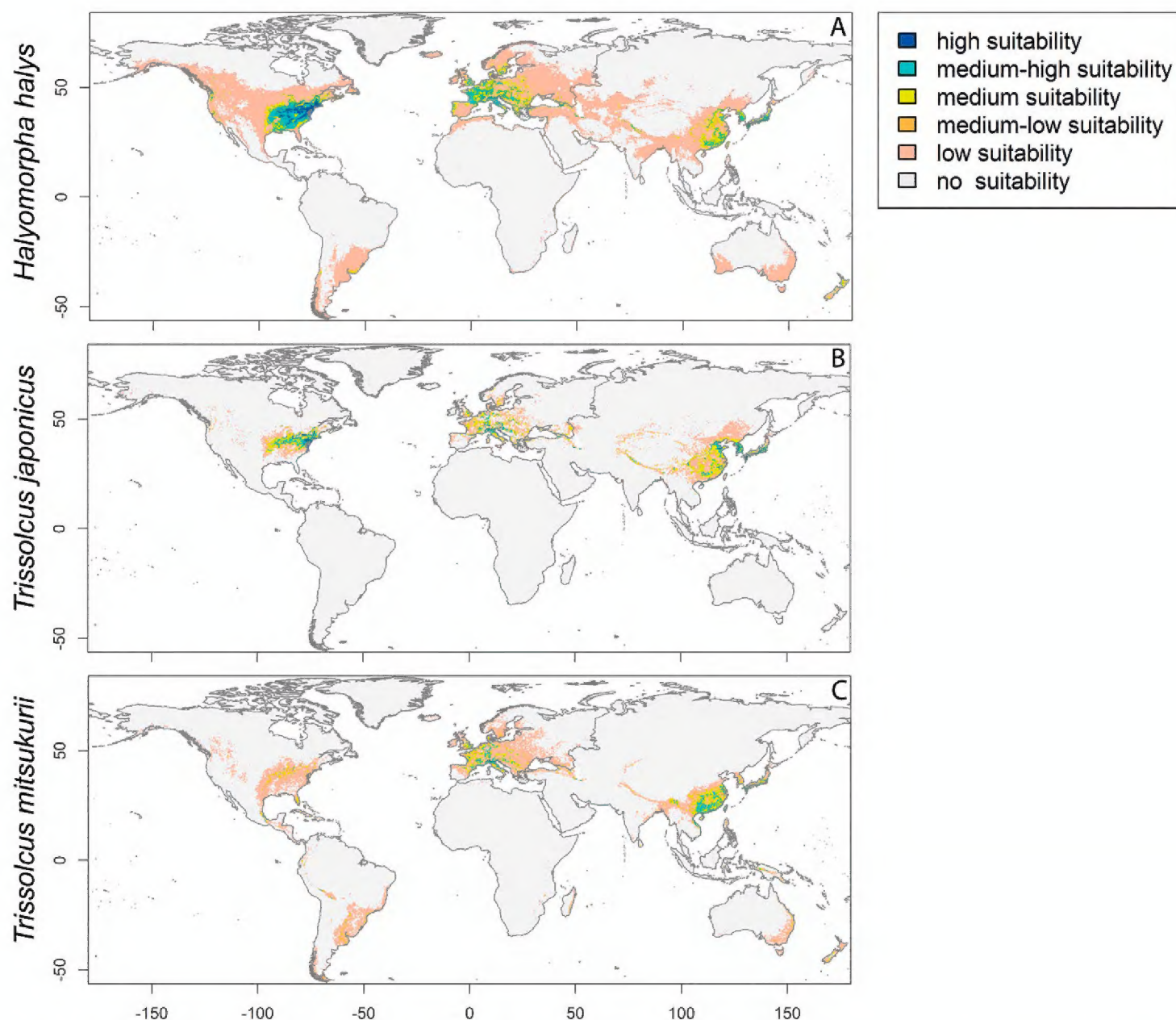
Figure 2. Habitat suitability for *Halyomorpha halys* (**A**), *Trissolcus japonicus* (**B**), and *T. mitsukurii* (**C**) at the global scale. Suitability is represented via six categories of increasing suitability, from no suitability (not suitable according to all five criteria) to high suitability (suitable according to all five criteria).

At the European scale, the entire study area was at least partially suitable for *H. halys* (Fig. 3A); nevertheless, the highest suitability occurred in France, Italy, Greece, and in scattered areas of Germany, the Netherlands, and the Balkan Peninsula. The main mountain chains and other areas in the extreme north and south are excluded from this large area. The patterns of the suitable areas for *T. japonicus* and *T. mitsukurii* were rather similar to each other and were also quite similar to the core areas for *H. halys* (Fig. 3B, C). However, a certain tendency of *T. japonicus* to prefer lower latitudes compared to *T. mitsukurii* was observed. The suitable areas for the former species were indeed mainly limited to the southern part of Europe, while those for the latter extended as far north as southern England, Denmark, Germany, and southern Sweden.

At the Italian scale, the most suitable areas for *H. halys* were basically restricted to the Venetian Plain, the central and western Po River Plain, the northern slope of the Tuscan-Emilian and Umbrian-Marchigian Apennines, and the Tuscan Hills (Fig. 4A). Nevertheless, areas with medium-high suitability extended these core areas as far south as Campania and in isolated spots in western Sardinia, eastern Sicily, eastern
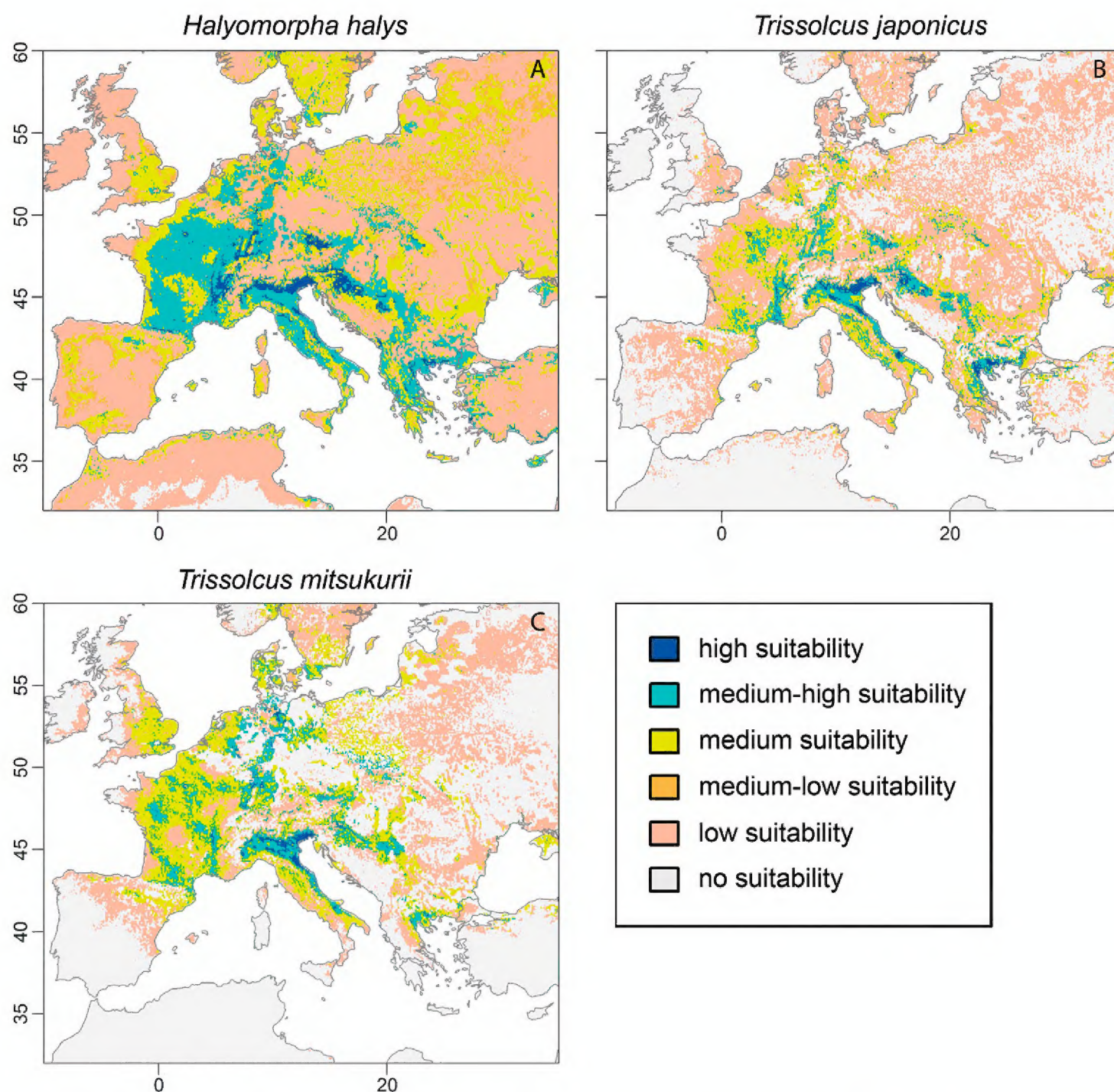
Figure 3. Habitat suitability for *Halyomorpha halys* (**A**), *Trissolcus japonicus* (**B**), and *T. mitsukurii* (**C**) at the European scale. Suitability is represented as six categories of increasing suitability, from no suitability (not suitable according to all five criteria) to high suitability (suitable according to all five criteria).

Calabria, and southern Apulia; in addition, most of the peninsula (with the exclusion of the highest mountain massifs) and Sardinia had medium suitability for the stink bug. As at the European scale, the patterns of the suitable areas for *T. japonicus* and *T. mitsukurii* were rather similar to each other and to the core areas for *H. halys* (Fig. 4B, C) but, even at the Italian scale, the tendency of the former species to prefer lower latitudes was evident.

The 'host-parasitoids co-suitability areas' basically reflect the core areas for suitability but some interesting differences can be evidenced. At the global scale, the East Asian core area for *H. halys* is surrounded by zones where the suitability for the parasitoids was good but the suitability for the stink bug was scarce. On the contrary, in the colonized zones in Europe and North America, the suitable area for *H. halys* was larger than the suitable zones for the two *Trissolcus* species (Fig. 5A and Suppl. material 3: table S3).
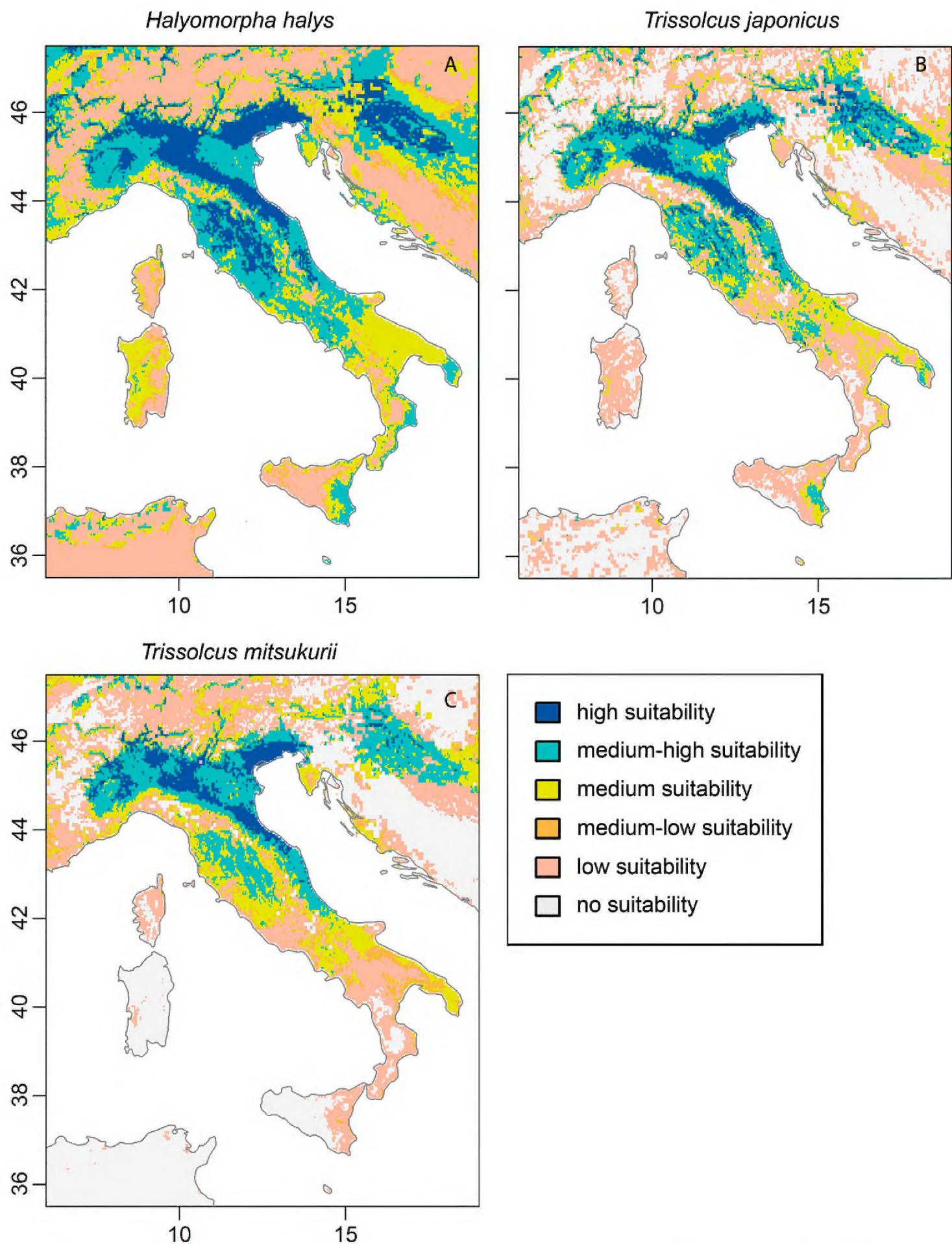
Figure 4. Habitat suitability for *Halyomorpha halys* (**A**), *Trissolcus japonicus* (**B**), and *T. mitsukurii* (**C**) at the Italian scale. Suitability is represented as six categories of increasing suitability, from no suitability (not suitable according to all five criteria) to high suitability (suitable according to all five criteria).

This was particularly true for the North American invaded range, where most of the suitable area for *H. halys* (especially in the south of the area) was not suitable for the two parasitoids. At the European scale, areas with good suitability for the stink bug and
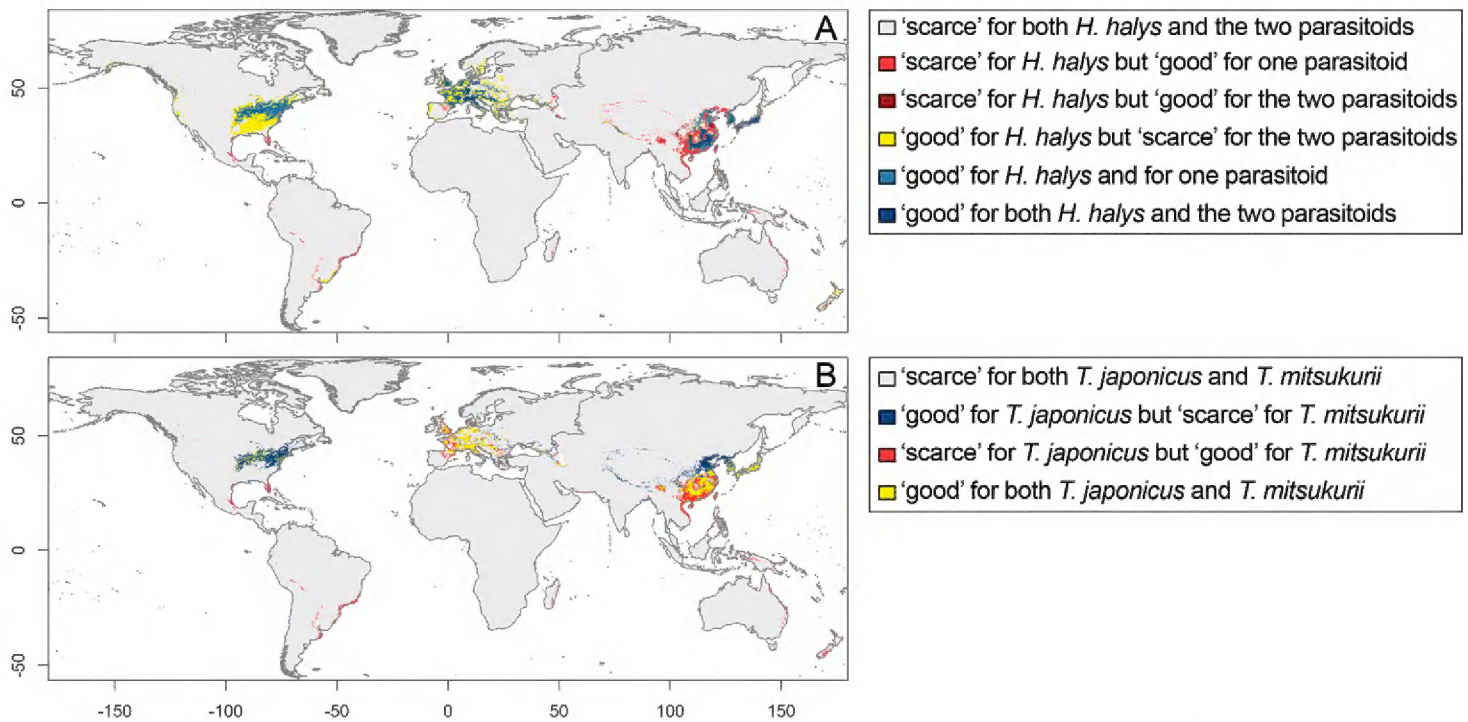
Figure 5. Map of the co-suitability of *Halyomorpha halys* and its two parasitoids (**A**) and the map of the co-suitability of *Trissolcus japonicus* and *T. mitsukurii* (**B**) at the global scale. Pixels are considered with scarce suitability if suitable according to less than three criteria and with good suitability if suitable according to three criteria or more.

the parasitoids were spread from northern Spain to eastern Ukraine and from southern Scandinavia to Sicily (Fig. 6A and Suppl. material 3: table S3). Nevertheless, many zones of this range, especially in the periphery, were suitable for *H. halys* but not for the *Trissolcus* species. On the contrary, few areas in northern Europe, northern and eastern Spain, northern Italy, and the Hungarian Plain were suitable for the *Trissolcus* species but not for *H. halys*. Similarly, at the Italian scale, the good contemporary suitability for the bug and its parasitoids corresponded approximately to the Po River Plain and the Venetian Plain, the Adriatic coast and the western slope of the north-central Apennines, the hills of Tuscany, northern Latium and Campania, and the Ionian coast (Fig. 7A and Suppl. material 3: table S3). Despite their suitability for *H. halys*, all the Apennines (the highest massifs excluded), the Tyrrhenian coast, and most of Sardinia and of the southern peninsular Italy were not suitable for *T. japonicus* and *T. mitsukurii*. On the other hand, a few zones on the Alps were suitable for the parasitoids but not for the stink bug.

As expected, the map of the co-suitability of *T. japonicus* and *T. mitsukurii* followed a similar general pattern as the previous maps. However, it provided interesting insights into the specificities of the two parasitoids. At the global scale, the suitable area was good for *T. japonicus* but not for *T. mitsukurii* in North America, and generally good for both the species in Europe, while in East Asia it was good for *T. japonicus* in the north, for both in the center, and for *T. mitsukurii* in the south (Fig. 5B and Suppl. material 3: table S3). In addition, small areas that were suitable for *T. mitsukurii* but not for *T. japonicus* also occur in the southern hemisphere (in South America, Madagascar, Australia, and New Zealand). At the European scale, the northern borders of the suitable area, such as in northern and western France, Belgium and the Netherlands,
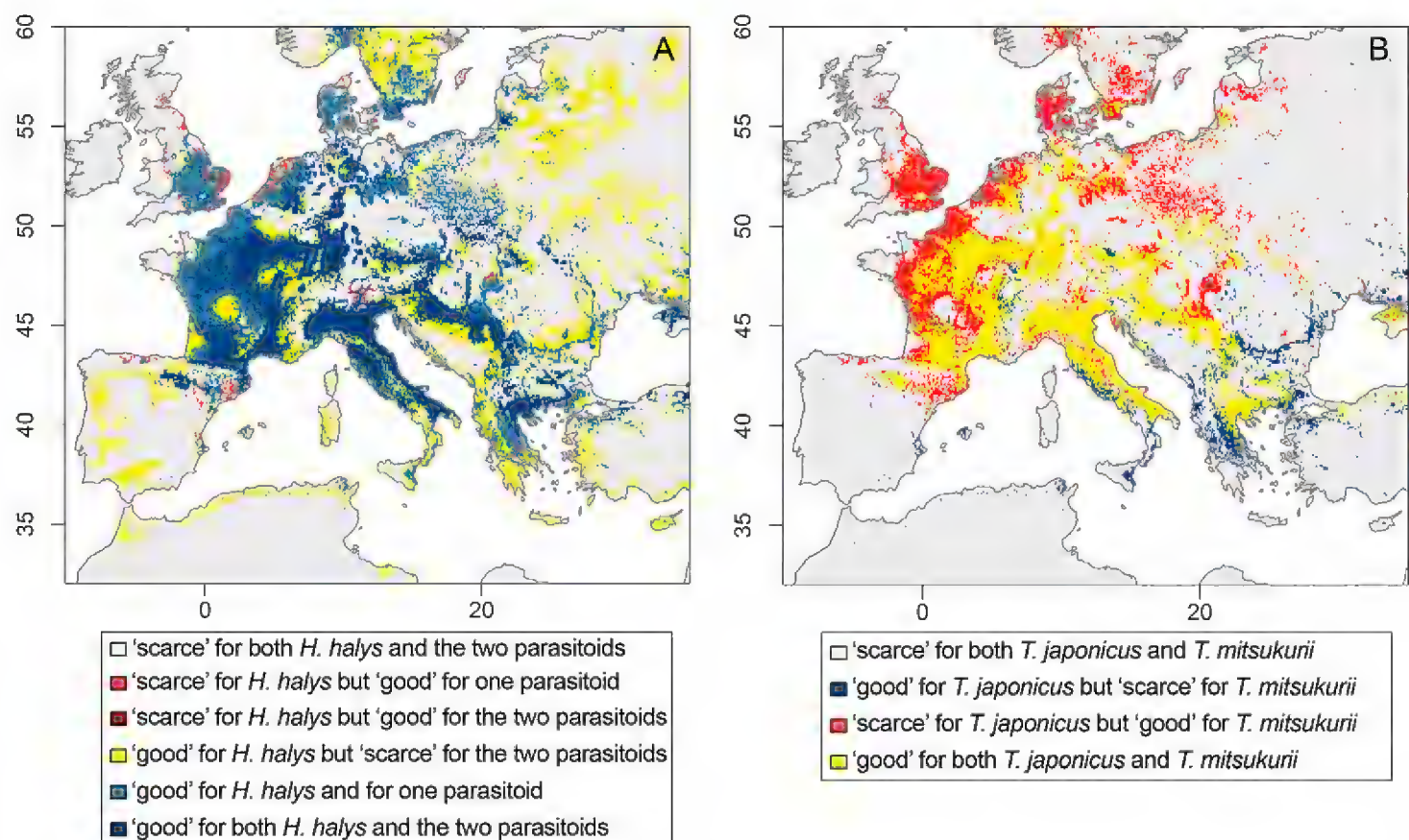
Figure 6. Map of the co-suitability of *Halyomorpha halys* and its two parasitoids (**A**) and the map of the co-suitability of *Trissolcus japonicus* and *T. mitsukurii* (**B**) at the European scale. Pixels are considered with scarce suitability if suitable according to less than three criteria and with good suitability if suitable according to three criteria or more.

Denmark, Germany, and Scandinavia, generally appeared good for *T. mitsukurii* only, the central part appeared good for both the species, while the southern borders, such as in southern Spain, central France, southern Italy, and Greece, generally appeared good for *T. japonicus* only (Fig. 6B and Suppl. material 3: table S3). The same general rule is also evident at the Italian scale, where the northern and upper boundaries along the Alps and Apennines were generally suitable for *T. mitsukurii* but not for *T. japonicus*, the core area was suitable for both the species, and the southern and lower boundaries in Sardinia, Sicily, and south-central peninsular Italy were suitable for *T. japonicus* only (Fig. 7B and Suppl. material 3: table S3).

Discussion

Model strength

A fundamental phase in species distribution modelling is the validation of the outputs, which measures how accurately the model predicts the presence or absence of the species. All our models have been 10-fold cross-validated; this means that each model was fitted 10 times with 90% of the available data, randomly chosen at each repetition, and used the remaining 10% as pseudo-independent data for validating the predictions. To
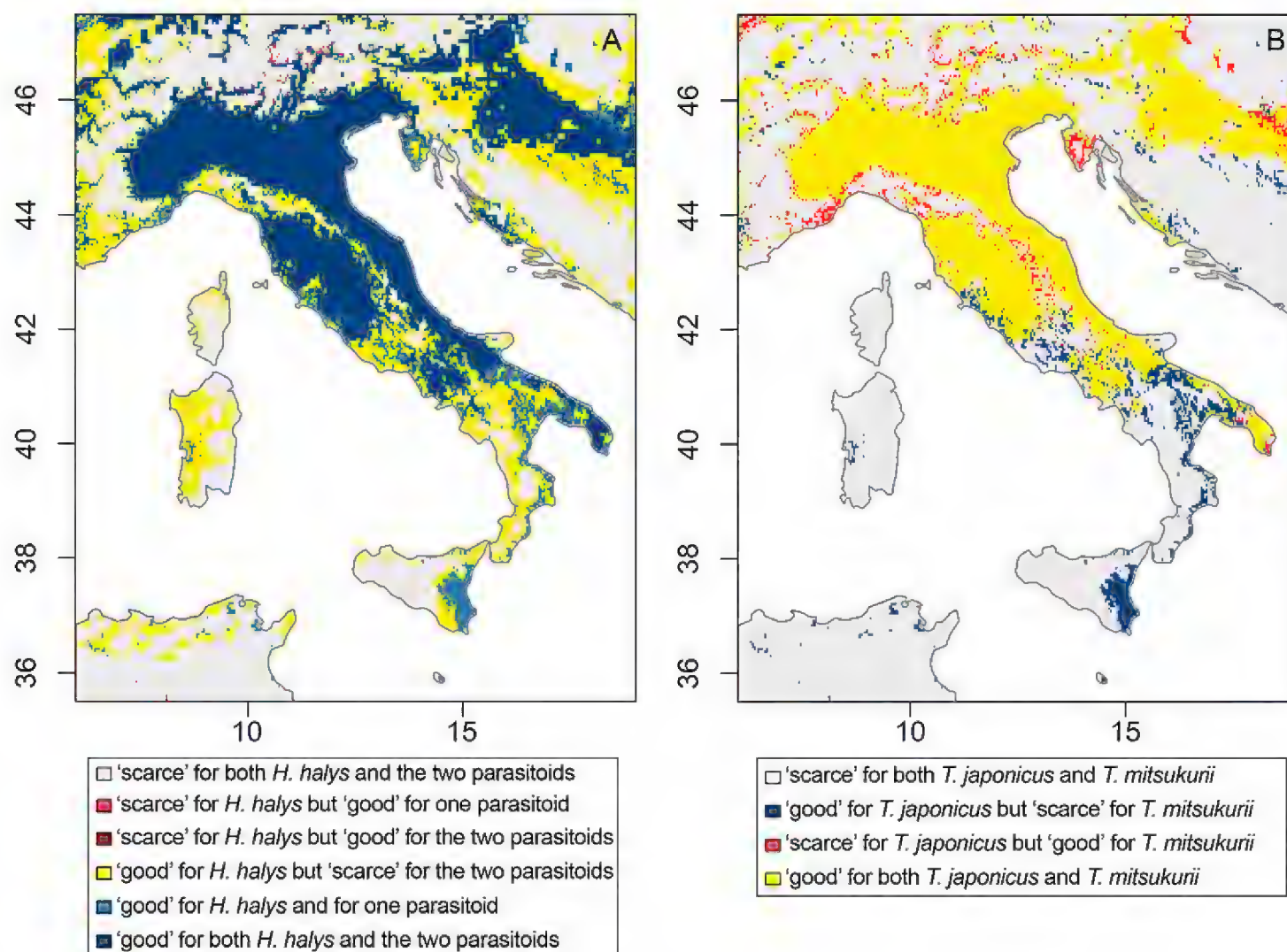
Figure 7. Map of the co-suitability of *Halyomorpha halys* and its two parasitoids (**A**) and the map of the co-suitability of *Trissolcus japonicus* and *T. mitsukurii* (**B**) at the Italian scale. Pixels are considered with scarce suitability if suitable according to less than three criteria and with good suitability if suitable according to three criteria or more.

do that, the true positive and the false positive rates (i.e., how many presence or absence points are correctly predicted) were measured for different thresholds, and the definite integral of this curve was calculated. This value represents the AUC index, which is one of the most frequently used methods for model validation and varies between 0 (no test point is correctly predicted) and 1 (100% of the test points are correctly predicted). In addition to this, we also calculated the Boyce index, which is an appropriate metric for presence-only models and varies between -1 and +1, with positive values indicating predictions that are consistent with the distribution of presences in the evaluation dataset (Hirzel et al. 2006). Our models obtained, on average, an AUC score of 0.987 (± 0.01) and a Boyce index of 0.994 (± 0.09), these results indicate an extremely high ability to predict the species presence/absence correctly.

An update of the potential distribution of *H. halys* and its parasitoids

While the GBIF dataset of *H. halys* can be considered robust, thanks to a large number of reliable records (citizens usually identified this stink bug with good accuracy),

the distributional data of *T. japonicus* and *T. mitsukurii* needed a careful review due to the high risk of misidentification. Avoiding erroneous data is, therefore, crucial. Consequently, we performed a detailed screening of the bibliographic records (Suppl. material 1: table S1), also taking into account the historical taxonomic complications presented by Talamas et al. (2017) and Buffington et al. (2018). The dataset was supplemented by many directly verified field collections.

As expected, the model of potential distribution of *H. halys* here proposed is similar to models previously estimated using both MaxEnt (Zhu et al. 2012) and CLIMEX (Kriticos et al. 2017; Yonow et al. 2021). At a global scale, our model shows lower suitability for expansion of this pest to tropical regions (Fig. 2A) than reported by using CLIMEX. At the European scale, compared with lower climate suitability proposed by Kriticos et al. (2017) and Yonow et al. (2021), our model shows that the habitat suitability for *H. halys* largely reaches a medium-high level (Fig. 2D) with patterns of high suitability in eastern France, northern Italy, Slovenia, and Croatia, as confirmed by several field studies (Hemala and Kment 2017; Streito et al. 2021; Delbac et al. 2022; Hess et al. 2022). In Italy, our model shows high potential suitability and distribution of the pest mainly in the north, aligning with observations of economic damage from previous studies (Bosco et al. 2018; Moraglio et al. 2018; Francati et al. 2021). The maps produced at different scales are not simple zooms of the same model. Rather, they are different models, fitted and projected at different resolutions. Thus, they used differently aggregated data and, as a consequence, their outputs are not perfectly identical. Nevertheless, the general pattern is congruent among different models.

Avila and Charles (2018) and Yonow et al. (2021) made assumptions on the potential distribution of *T. japonicus* – also supported by data on the wasp distribution in North America and Europe (Talamas et al. 2015; Milnes et al. 2016; Sabbatini Peverieri et al. 2018; Abram et al. 2019; Stahl et al. 2019b) – resulting in a similar finding as reported by our study, except for Spain and the entire Mediterranean coast, where our model indicates low or no suitability.

According to our results, *T. mitsukurii* has a broad, but low, suitability in Australia, New Zealand, North and South America (Fig. 2C). Nevertheless, the potential suitable extent we predicted is more limited with respect to the assumptions provided in a previous study (Yonow et al. 2021). The rapid expansion of adventive populations of *T. mitsukurii* in Europe (Sabbatini Peverieri et al. 2018; Scaccini et al. 2020; Bout et al. 2021; Rot et al. 2021; Mele et al. 2022) confirmed our hypothesis of a high level of potential habitat suitability: this species has the potential to spread throughout Europe and beyond.

In Italy, *T. japonicus* shows greater potential for range expansion at lower latitudes in southern Italy and the islands of Sardinia and Sicily than *T. mitsukurii*, due to denser patterns from medium to high habitat suitability (Fig. 4B, C). The expectation for the future could be the potential spread of both species in these areas, even considering the current presence at lower latitudes of *H. halys* (Cianferoni et al. 2018; Tassini and Mifsud 2019).

Co-suitability maps: a tool for control applications

The co-suitability map of parasitoids against *H. halys* at a global scale (Fig. 5A) shows that areas with good suitability for *H. halys* and scarce suitability for *Trissolcus* spp. are absent in the Asian region where, instead, there is a predominance of areas with good suitability for the host and for one or two parasitoids (marked with light blue and dark blue patterns, respectively), and areas with scarce suitability for *H. halys* but good suitability for one or two parasitoids (marked with light red and dark red patterns, respectively). The lack of yellow zones (i.e., good suitability for *H. halys* but scarce for *Trissolcus* spp.) in the Asian region means that the host distribution area completely overlaps the suitable areas of the parasitoids. It is possible that the two parasitoids and their host, all native to eastern Asia, show a more complex interspecific interaction. In native areas, the two parasitoids are able to exploit a larger host range (Zhang et al. 2017). Confirming this, in Australia, where *H. halys* was only intercepted and eradicated (Horwood et al. 2019; Hess et al. 2022), and shows low suitability (Fig. 2A), the presence of *T. mitsukurii* has been known since at least 1914 (Caron et al. 2021), suggesting the possible establishment of this parasitoid by exploiting other yet unknown hosts. Concerning *T. japonicus*, information on possible secondary hosts in the new areas in Europe and the United States is still scarce (Haye et al. 2020; Moraglio et al. 2020; Zapponi et al. 2021). Certainly, further investigations are needed to identify possible secondary hosts of both parasitoids, especially to assess their attractiveness in comparison with the coevolved host and, consequently, to track the new interactions that will be established in favorable areas for parasitoid establishment.

The areas where one or both parasitoids show suitability to coexist with *H. halys* (marked with light blue pattern and with dark blue pattern, respectively; Fig. 5A) reveal good chances of success in controlling the pest using them as BCAs. This means that the use of either one of the two parasitoids (light blue pattern, in the map) or both (dark blue pattern) can be effective in controlling *H. halys* depending on the individual habitat suitability (Fig. 2). *Trissolcus japonicus* shows a higher potential habitat suitability than *T. mitsukurii* at a global scale (Fig. 2B, C). Moreover, in Europe and Italy, where more structured surveys of the two parasitoids were performed (Zapponi et al. 2021), and according to the co-suitability map (Fig. 6), *T. japonicus* shows greater potential suitability than *T. mitsukurii* at lower latitudes. Therefore, these results further support the decision to field release *T. japonicus* as a part of a three-year national program initiated in northern Italy and extended throughout the peninsula (MATTM 2020). In light of the parasitoid co-suitability map (Fig. 6), the recent proposal to release *T. mitsukurii* against *H. halys* in the Northwest of France (Martel G., Hamidi, R., Thomas M., ANPN-RIPPOSTE, Région Nouvelle-Aquitaine, France, N° 15994520), in the area where this parasitoid was found in 2020 (Bout et al. 2021), appears to be the best solution considering its higher suitability, especially if compared with the lower suitability of *T. japonicus* in most of that country.

The predominance of the yellow and blue pattern (Fig. 5B) in the adventive range in Europe and North America suggests the possibility of successfully using one of the two *Trissolcus* species as a BCA, also from the perspective of a classical biological control

program. To optimize the success of any BCA at the local scale, this model should be supplemented with an assessment of the local climatic parameters best suited to the parasitoid species. In particular, this is even more important in areas characterized by high habitat richness, in terms of geographic and climate variables (Cervellini et al. 2021), such as in the Iberian and Scandinavian peninsulas, eastern Europe, southern Greece (Fig. 6B), and, at Italian scale, in Sardinia and most of southern peninsular Italy (Fig. 7B).

Environmental factors play an important role in the performance of a BCA, because they can determine the success of any biological control program. Therefore, preliminary studies on the species habitat suitability can help to choose better performing BCAs to introduce into an ecosystem in a classical biological control program. Predicting suitable ecological niches for *H. halys* and its two parasitoids is a critical approach for crop management and biological control of this pest. The suitable core areas for *T. japonicus* and *T. mitsukurii* are quite similar to each other. The niches of these species are generally smaller than the area indicated by model-based predictions, and this is due to, among others, climatic variables that are not the only determinants of habitat suitability. Several natural and anthropogenic factors can also influence the potential habitat distribution of these species as well as their interaction. Therefore, the information provided by the model can help in the selection of the parasitoid to be used in relation to the suitability of the area, but it will still need to be substantially validated through field surveys, which can also further document the spatial intensities of the parasitoid species in potentially suitable areas.

CRediT authorship contribution statement

Francesco Tortorici: Conceptualization, Data curation, Species identification, Investigation, Methodology, Software, Writing – Original draft. **Pierluigi Bombi:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – Original draft. **Laura Loru:** Funding acquisition, Resources Supervision, Writing – Review and Editing. **Alberto Mele:** Species identification, Investigation, Writing – Review and Editing. **Silvia Teresa Moraglio:** Investigation, Writing – Original draft. **Davide Scaccini:** Data curation, Species identification, Investigation, Writing – Review and Editing. **Alberto Pozzebon:** Funding acquisition, Resources Supervision, Writing – Review and Editing. **Roberto Antonio Pantaleoni:** Conceptualization, Funding acquisition, Resources Supervision, Writing – Original draft. **Luciana Tavella:** Conceptualization, Funding acquisition, Resources Supervision, Writing – Original draft. All authors have read and agreed to the published version of the manuscript.

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Supplementary material 1

List of references including geographic records of *Trissolcus japonicus* and *T. mitsukurii* distribution
Authors: Francesco Tortorici, Pierluigi Bombi, Laura Loru, Alberto Mele, Silvia Teresa Moraglio, Davide Scaccini, Alberto Pozzebon, Roberto Antonio Pantaleoni, Luciana Tavella
Data type: references
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Link: https://doi.org/10.3897/neobiota.85.102501.suppl1

Supplementary material 2

Variance Inflation Factors for the variables included in the models at the three scales
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Data type: table (pdf file)
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Link: https://doi.org/10.3897/neobiota.85.102501.suppl2

Supplementary material 3

Percentage of surface of each continent/country/region in the different conditions
Authors: Francesco Tortorici, Pierluigi Bombi, Laura Loru, Alberto Mele, Silvia Teresa Moraglio, Davide Scaccini, Alberto Pozzebon, Roberto Antonio Pantaleoni, Luciana Tavella
Data type: table (pdf file)
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Link: https://doi.org/10.3897/neobiota.85.102501.suppl3

Supplementary material 4

Map of global distribution of locations recorded for *H. halys*, *T. japonicus* and *T. mitsukurii*

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Data type: occurrences

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